

Systematics and relationships of the bigeneric Pacific family *Campynemataceae* (Liliales)

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Summary : *Campynemataceae* comprises two genera, the monotypic *Campynema* from Tasmania, and *Campynemanthe*, with three species, endemic to New Caledonia. Family characteristics are a basic lilialean ground plan with flowers with six similar, greenish accrescent and persistent tepals, six stamens with extrorse anthers and an inferior ovary with free stylodia. The two genera have in the past been assigned to *Iridaceae*, *Amaryllidaceae* or *Hypoxidaceae* but are shown to be unrelated to these families on embryological and morphological grounds. *Campynemataceae* are suggested to be most closely allied with *Melanthiaceae*. *Campynema* has fleshy roots produced from a root crown, a single basal leaf with an acute apex and a flowering stem with a simple 1-3-flowered inflorescence. *Campynemanthe* has a persistent rhizome, fibrous roots, several basal leaves with tridentate apices and a compound semi-umbellate inflorescence. *Campynemanthe neocaledonica* is transferred from *Campynema* with which it disagrees in all significant features, while the new species *C. parva* is described.

Résumé : Les *Campynemataceae* comprennent deux genres, *Campynema*, genre monotypique de Tasmanie, et *Campynemanthe*, qui a trois espèces et est endémique de la Nouvelle-Calédonie. Les caractéristiques de la famille sont essentiellement celles des Liliales : des fleurs aux six tépales semblables, verdâtres, accrescentes et persistentes, six étamines avec des anthères extrorses, et un ovaire infère aux stylodes libres. Les deux genres ont été autrefois inclus dans les *Iridaceae*, *Amaryllidaceae* ou *Hypoxidaceae*, mais d'après des données embryologiques et morphologiques présentées ici ils n'ont aucun rapport avec ces familles. Il est suggéré que les *Campynemataceae* sont plus étroitement liées aux *Melanthiaceae*. Le genre *Campynema* a des racines charnues produites à partir d'une couronne, une seule feuille basale avec un apex aigu, et une tige fertile avec une inflorescence simple à 1-3 fleurs. Le genre *Campynemanthe* a un rhizome persistant, des racines fibreuses, plusieurs feuilles basales à apex tridenté, et une inflorescence composée semi-ombelliforme. Le *Campynemanthe neocaledonica* est transféré du genre *Campynema* duquel il diffère par tous les caractères importants. Une nouvelle espèce, *Campynemanthe parva*, est décrite.

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INTRODUCTION

Campynemanthe and *Campynema* are two Pacific genera of restricted distribution in New Caledonia and Tasmania respectively. They are generally believed to be closely allied but their relationships within a variously circumscribed Liliales or Liliiflorae are uncertain.

In addition the circumscription of the two genera has until now been inconsistent with the morphology of the species. The genera have a basic liliifloran ground plan with a rhizomatous to tufted rootstock, one or several, basally clustered leaves, a well defined flowering stem, trimerous flowers with six similar tepals and six stamens, and large seeds with a brown testa. They differ from most Liliales in having an inferior ovary, free stylodia, and they share in addition similar, greenish, non-patterned persistent accrescent tepals that enlarge considerably as the fruit develops.

The two genera have been assigned to various families, initially to their own *Campynemataceae* (DUMORTIER, 1829), and subsequently to *Iridaceae* (BENTHAM & HOOKER, 1873; TAKHTAJAN, 1980), *Amaryllidaceae* (PAX, 1888; PAX & HOFFMANN, 1930) or *Hypoxidaceae* (HUTCHINSON, 1959; MELCHIOR, 1964). Most recently, as a result of critical embryological study (DAHLGREN & LU, 1985) a strong argument has been advanced for considering the two genera as members of, or very close to *Melanthiaceae*, in Melanthiales, a segregate of Liliales. They further suggest that *Campynemataceae* may be closer to the achlorophyllous *Protolirion* and *Petrosavia* than to other members of *Melanthiaceae*.

Campynema has usually been treated as ditypic with the Tasmanian *C. lineare* and *C. neocaledonicum* in New Caledonia, while *Campynemanthe* has been regarded as a monotypic New Caledonian endemic. A superficial examination of the three species reveals that *Campynema neocaledonicum* closely resembles *Campynemanthe*. The reason for separating them in different genera is apparently due to the pauciovulate ovary in *Campynemanthe* and multiovulate ovary in *Campynema*. The difference is not as significant as believed in the past and is outweighed by several shared features of *C. neocaledonicum* and *Campynemanthe* not found in the Tasmanian *Campynema lineare*. *Campynema neocaledonicum* must be transferred to *Campynemanthe*, leaving *Campynema* a Tasmanian monotype. *Campynemanthe*, entirely restricted to New Caledonia, has two known species and one more is described in this paper. The characteristics of *Campynema* and *Campynemanthe* are outlined below, followed by a discussion of the possible familial relationships of the genera. A systematic revision of *Campynemanthe* and a review of *Campynema* concludes this paper.

GENERAL MORPHOLOGY AND EMBRYOLOGY

Campynemanthe and *Campynema* are small herbaceous plants with basally clustered mesomorphic leaves (one basal leaf in *Campynema*) borne on a short ascending persistent rhizome (*Campynemanthe*) or a tufted crown (*Campynema*). The leaves have open sheaths, and are dorsiventral, slender and lanceolate to linear. They are unusual in *Campynemanthe* in having a 3-dentate apex with subequal to very unequal teeth. Leaves and probably other tissues too, contain calcium oxalate raphide bundles in special idioblasts (GOLDBLATT et al., 1984), in marked contrast to *Iridaceae* which have styloid calcium oxalate crystals in 74 of 75 genera examined, and uniformly lack raphide bundles. *Campynema* lacks vessels in the shoot system, and has very primitive vessels (or possibly lacks vessels entirely) in the roots (CHEADLE, 1968). The condition in *Campynemanthe* is not known.

The flowering stem is well developed and bears few to several reduced leaves that become progressively smaller upward. In *Campynemanthe* the flowers are clustered in an umbel-like inflorescence consisting of several few-flowered units (see also DAHLGREN & LU, 1985), each with a larger basal bract and a smaller one at the bases of the pedicels. The inflorescence of *Campynema* consists of one to three flowers, the lateral if present on long pedicels produced in the axils of small bracts. The pedicels of the lateral flowers only, have small abaxial bracteoles inserted shortly below the flowers.

The flowers are small and greenish in color. The six tepals and six stamens, each arranged in two whorls, and three carpels are typical for Liliales but the genera stand out in having an inferior ovary and free stylodia. The tepals are unusually persistent and continue to enlarge after fertilization, finally in the fruit about half again to twice as large as at anthesis. Both *C. neocaledonica* and *C. viridiflora* have conspicuous dull yellow thickened areas in the lower half of the tepals which very likely represent tepal nectaries. According to DAHLGREN & LU (1985), *Campynemanthe* does not have septal nectaries.

The ovary is very small and difficult to see at anthesis but after fertilization, it can easily be recognized. It is 3-locular and the placentation is axile (DUTT, 1970 ; DAHLGREN & LU, 1985 ; pers. obs. on developing fruit). The ovules are relatively few in *Campynemanthe*, 4 to 10 or more per locule, depending on the species, and many in *Campynema*. The stamens are small in both genera and the anthers 4-sporangiate with basically extrorse dehiscence, but tending to latrorse especially in *Campynemanthe*. In *Campynema* the stamens curve outwards during anthesis, the generic name alluding to this feature.

Campynemataceae are relatively well known embryologically as a result of studies by DUTT (1970) on *Campynema* and DAHLGREN & LU (1985) on *Campynemanthe*. The embryology is essentially similar in both genera. The microsporangium wall is 4-layered, with a conspicuous endothecium under the epidermis. The middle layer is largely crushed but persists at least in *Campynemanthe* until late meiosis. The tapetum is typical for Liliales in being secretory (and markedly different from the amoeboid tapetum of *Hypoxidaceae*). The tapetal cells are 2-nucleate in *Campynemanthe* and according to DUTT, multi-nucleate in *Campynema*. Microsporogenesis is successive in both genera (in contrast to simultaneous in *Iridaceae*). The pollen grains are shed singly and are inaperturate in *Campynemanthe* (ERDTMAN, 1952 ; DAHLGREN & LU, 1985) and sulcate in *Campynema* (ERDTMAN, 1952 ; DUTT, 1970).

The ovules are anatropous, bitegmic, weakly crassinucellate, and borne on axile placentas. The micropyle is formed only by the inner integument in both genera. A parietal cell is formed from the archesporium and gives rise to a parietal tissue. The nucellar epidermis in *Campynemanthe* also divides periclinally and becomes 2-layered. The embryo sac is of the Polygonum type (not known completely in *Campynemanthe*).

The seeds (known in detail only in *Campynemanthe*) have a brown coat and a testa formed by the inner and outer integuments (HUBER, 1969). The peculiar black phytomelan pigment characteristic of most non-bacciferous Asparagales (*sensu* DAHLGREN & CLIFFORD, 1982) is completely lacking in *Campynemataceae* in contrast to *Hypoxidaceae* and *Amaryllidaceae*. The seeds are nearly globose to angular in *Campynemanthe* and have long persistent funicles but in *Campynema* the seeds are flattened, sometimes almost discoid, and have a spongy outer coat. Endosperm formation has not been recorded for either *Campynema* or *Campynemanthe*. It would be interesting to know whether it is nuclear as in virtually

all Liliales (*sensu* DAHLGREN et al., 1985) or helobial as in *Melanthiaceae*, assigned to Melanthiales by DAHLGREN et al. (1985) together with *Campynemaceae*. Seed storage products are hemicellulose, which is abundant in the thick and conspicuously pitted cell walls (HUBER, 1969), and fatty oils. HUBER considers the seed structure to be very similar to *Iridaceae-Iridoideae* in all details. This may be due to convergence or simply to shared primitive characteristics, but probably does not imply close relationship. The embryo is minute, 1/9 the length of the endosperm, in contrast to most *Iridaceae* including the genera which have the most similar seeds.

RELATIONSHIPS

Campynemanthe was not assigned to a family when first described, and BAILLON (1893) was uncertain about its affinities, discussing its similarities with several Lilialean groups. DUMORTIER (1829) was the first to assign *Campynema* to family and erected *Campynemataceae* for the single species. Subsequent workers ignored or were unaware of *Campynemataceae*, and BENTHAM (1873) initially assigned the genus to *Iridaceae* in the *Flora Australiensis*. Later, in the *Genera Plantarum* (BENTHAM & HOOKER, 1883), he treated it as a member of *Amaryllidaceae* tribe *Hypoxideae*, commenting that its seed, extrorse anthers, and free stylodia were discordant in the family. In the first edition of *Die Natürliche Pflanzenfamilien*, PAX (1888 : 124) treated *Campynema* as the sole member of *Campynematoideae* of *Amaryllidaceae*, a heterogeneous family in which he included mostly as subfamilies, *Agavaceae*, *Alstroemeriaceae*, *Tecophilaeaceae*, some genera of *Haemodoraceae*, and *Hypoxidaceae*, united mainly by an inferior ovary. The treatment in the second edition is similar (PAX & HOFFMANN, 1930) except that *Campynemanthe* is included in *Campynematoideae*. HUTCHINSON (1959) and MELCHIOR (1964) include the two genera in *Hypoxidaceae*.

The resemblance between *Campynemataceae* and *Amaryllidaceae* is entirely superficial, and the two were seen as related because of the hypogynous flower combined with an apparently umbel-like inflorescence in *Campynemanthe*, which DAHLGREN & LU (1985) point out is a compound and branched structure and not at all like the umbel of *Amaryllidaceae*, which in addition have a true scape, i.e. a flowering stem without leaves, and a bulb. The seeds of *Amaryllidaceae* and *Hypoxidaceae* are also quite different from those of *Campynemataceae* in having a black phytomelan layer in the testa (at least in species with capsular fruits), a difference noted by BENTHAM & HOOKER (1883), who included *Campynema* with a query, in *Amaryllidaceae-Hypoxidoideae*. Other primary characters of *Amaryllidaceae* and *Hypoxidaceae* different from those in *Campynemataceae* are the completely fused style and the introrse anthers and, in *Hypoxidaceae*, the absence of a parietal cell and the amoeboid tapetum (DE VOS, 1961 ; DAHLGREN & LU, 1985).

Recent work by DAHLGREN & CLIFFORD (1982) and DAHLGREN & RASMUSSEN (1983) places *Campynemataceae* close to or in *Colchicaceae*, in which similar seeds and free stylodia occur. *Colchicaceae*, however, have hypogynous flowers, often very distinctive alkaloids, and some genera are now known to have calcium oxalate crystals in the form of crystal sand (GOLDBLATT et al., 1984). They also differ embryologically in lacking a parie-

tal cell and are probably not closely related to *Campynemataceae*. Critical embryological and morphological study by DAHLGREN & LU (1985) seems to confirm that *Campynemataceae* are probably not related at all to *Iridaceae*. The shared hypogynous flower is due to convergence, and in fact the primitive condition for *Iridaceae* is most likely an epigynous flower (in the monotypic *Isophysis*) (GOLDBLATT et al., 1984). *Iridaceae* also differ from *Campynemataceae* in their ensiform monofacial leaves, primitively fugaceous tepals (persistent and accrescent in *Campynemataceae*), simultaneous microsporogenesis, and calcium oxalate styloids (typical raphides bundles are present in *Campynemataceae*) (GOLDBLATT et al., 1984). It seems that the two families share no apomorphic characters at all, or at least none that are not shared by several other Lililean families. The seed similarities between *Campynemanthe* and *Iridaceae* stressed by HUBER (1969), must be viewed either as due to convergence or as shared symplesiomorphic features.

Most recently DAHLGREN et al. (1984) and DAHLGREN & LU (1985) associate *Campynemataceae* with *Melanthiaceae*, either close to or in this family which they segregate in Melanthiales. The primary characteristics of *Melanthiaceae* are consistent with such a treatment for *Melanthiaceae* have a rhizome, the anthers are usually extrorse, the tapetum glandular, the microsporogenesis successive, many species have raphide bundles (AMBROSE, 1980), and the seeds lack phytomelan. *Campynemataceae* differ from *Melanthiaceae* in their hypogynous flower, relatively large seeds, and in *Campynemanthe*, inaperturate pollen grains, 3-dentate leaf apex, and somewhat umbel-like inflorescence (DAHLGREN & LU, 1985). The seeds also cannot be matched exactly in *Melanthiaceae*. I suggest that *Campynemataceae* remain a separate family, and be considered a member of Melanthiales close to *Melanthiaceae*, but specialized in its seed morphology and inferior ovary. Other differences such as the single leaf and spongy outer seed coat of *Campynema* and the 3-dentate leaf apex, inaperturate pollen and umbel-like inflorescence of *Campynemanthe*, seem of a less fundamental nature but are also consistent with its more complex and apparently specialized morphology.

SYSTEMATICS

1. CAMPYNEMANTHE Baillon

Bull. Mens. Soc. Linn. Paris 2 : 1106 (1893) ; Hist. Pl. 12 : 592 (1894) ; PAX & HOFFMANN, Natürl. Pflanzenf., ed. 2, 15a : 430 (1930) ; DAHLGREN & LU, 1985.

Plants evergreen perennials with a prostrate to ascending, relatively short rhizome and a basal rosette of crowded erect strap-like leaves. Rhizome short, thick, fibrous, ascending to \pm erect above, covered by the decaying and membranous bases of the basal leaves. Leaves dorsiventral, many, erect to ascending, linear, lacking a midrib, apically 3-fid, the central tooth either longer, as long, or shorter than the laterals. Flowering stems lateral, single or up to 4, unbranched, erect, bearing reduced and progressively smaller leaves above, these apically entire. Inflorescence umbel-like with the flowers clustered towards the apex of the flowering stem, consisting of a few units each with a larger basal bract and

a smaller bract at the base of the pedicels. Flowers greenish, with six tepals in two whorls ; tepals free, persistent, enlarging during fruit development ; linear to ovate, with a pad of ? secretory tissue in the lower half. Stamens six, inserted at the base of the tepals ; filaments slender, erect ; anthers basifixed, oblong to globose, dehiscent extrorsely (-weakly latrorsely) by longitudinal slits. Ovary hardly swollen at anthesis, obconic, partly to entirely inferior, 3-locular, placentation axile ; ovules (2-)4 to several per locule ; stylodia short, tapering, contiguous below and united at the base, recurved above and ultimately stigmatic. Fruit a capsule, walls more or less membranous, dehiscent by decay of the lateral or dorsal walls, the seeds remaining attached to the placentas for a time ; seeds brown, surface obscurely reticulate, weakly to strongly angular, funicles persistent ; embryo minute.

TYPE : *C. viridiflora* Baillon.

SPECIES : 3, restricted to New Caledonia.

KEY TO CAMPYNEMANTHE

- 1a. Flowers small, at time of pollination the tepals up 1.8-2 mm long, later increasing in fruit to 3 mm ; flowering stems about as long or more often exceeding the leaves ; inflorescences usually with 7-25 flowers ; pedicels 0.8-2 cm long (-3 cm in fruit) ; capsule 2-3 mm long \times 3-6 mm wide ; foliage leaf apices 3-fid with the central tooth very short or about as long to somewhat longer than the lateral teeth.
 - 2a. Flowering stems usually exceeding the leaves ; inflorescences usually with 15-25 flowers ; seeds globose-angular, ca. 1.8 mm in diam. ; leaf apex with the central tooth always much shorter than the lateral teeth..... *C. viridiflora*
 - 2b. Flowering stems usually about as long as the leaves ; inflorescences with 7-15 flowers ; seeds angular-elongate, ca. 1 mm long \times 0.5 mm wide ; leaf apex with the central tooth about as long to somewhat longer than the lateral teeth..... *C. parva*
- 1b. Flowers relatively large, at anthesis the tepals 4-6 mm long \times 3 mm wide enlarging in fruit to 7-8 mm ; flowering stems usually shorter than the leaves ; inflorescences with 3-10(-15) flowers ; pedicels 2-4 cm long (4-6 cm in fruit) ; capsule 5-6 mm long \times 4-6 mm wide ; seeds angular-elongate (subfusiform) ca. 2 mm long \times 1-1.4 mm wide ; leaf apices 3-fid with the central tooth much longer than the lateral teeth..... *C. neocaledonica*

1. *Campynemanthe neocaledonica* (Rendle) Goldblatt, *comb. nov.*

Campynema neocaledonicum RENDLE, J. Linn. Soc., Bot. 45 : 256 (1921) ; GUILLAUMIN, Fl. anal. et synopt. Nouvelle-Calédonie : 55 (1948).

LECTOTYPE (here designated) : *Compton 1811*, New Caledonia, Ignambi, forest at 3500 ft (BM).

Plants 18-25 cm high. Rhizome relatively thick, to 5 mm in diameter. Leaves up to 35 cm long, 3-6 mm wide, apices 3-fid, the central tooth much exceeding the laterals. Flowering stem shorter than the leaves (occ. nearly as long to slightly longer), 15-18(-30) cm long. Inflorescence with 3-10(-15) flowers ; bracts 10-20 mm long, bracteoles 8-12 mm long ; pedicels 2-3 cm long, elongating to 3-4 cm or more in fruit. Flowers relatively large, green with orange markings on the lower part of the tepals (? = nectaries), sometimes

purple on the reverse of the tepals ; tepals on opening 4-6 mm long, about 3 mm wide, enlarging to 7-8 mm long in fruit. Filaments about 1 mm long ; anthers oblong (- ± ovate), 1 mm long, pollen yellow. Ovary about 1.8 mm long, ovules several per locule, in 2-3 rows ; stylodia about 2.5 mm long. Capsules 5-6 mm long, 4-6 mm wide, 3-gonous, the angles obscurely winged, the walls becoming membranous and disintegrating, the remaining seeds exposed on the persistent placentas ; seeds angular, about 2 mm long, 1-1.4 mm wide ; 10 or more per locule, in 2 rows.

DIAGNOSTIC FEATURES

Campynemanthe neocaledonica is readily distinguished by its larger flower with tepals on opening 3-4 mm long and in the fruit 7-8 mm long. Also the capsules are larger than in the other species, and 5-6 mm long, with several angular seeds in each locule of the ovary. In general aspect, *C. neocaledonica* can be recognized by its broad leaves, 3-6 mm wide, that are usually longer than the flowering stems and have a central apical tooth conspicuously longer than the laterals. The differences are several and it is unlikely to be confused with the other species.

HISTORY

The species was apparently first discovered by Benedict BALANSA in 1869 when New Caledonia was first explored botanically. However, it was only after R. H. COMPTON collected it at Ignambi and Mt Panié during his visit to New Caledonia in 1914 that it was described. It was referred to *Campynema* by RENDLE (1921), apparently due to the superficial similarity to the Tasmanian *C. lineare*, in its numerous ovules and seeds. Although RENDLE was aware of *Campynemanthe viridis* when he described *Campynema neocaledonicum*, he did not elaborate the relationships of these species. This treatment was followed uncritically by GUILLAUMIN (1948) who distinguished *Campynema* from *Campynemanthe* on the basis of the ovary shape and number of seeds per locule.

As outlined in the introduction, *Campynemanthe neocaledonica* has more than just a general morphological similarity to *C. viridis*. It has a persistent rhizome, the same type of semi-umbellate inflorescence, relatively short fruit, numerous leaves with remarkable 3-dentate apices, and a similar seed structure to that found in *C. viridis*.

DISTRIBUTION AND ECOLOGY

Campynemanthe neocaledonica is widespread on New Caledonia in moist forested sites at higher elevations and it extends from Mt Ignambi and Mt Panié in the north to the Plateau de Dogny near the center of the island (Fig. 1). A peculiar form, at present best attributed to this species occurs on Montagne des Sources and Mt Mou in the far south where both *C. viridiflora* and *C. parva* are found. This form has stems slightly exceeding the leaves, inflorescences with few flowers, and the central tooth of the leaf apex is usually

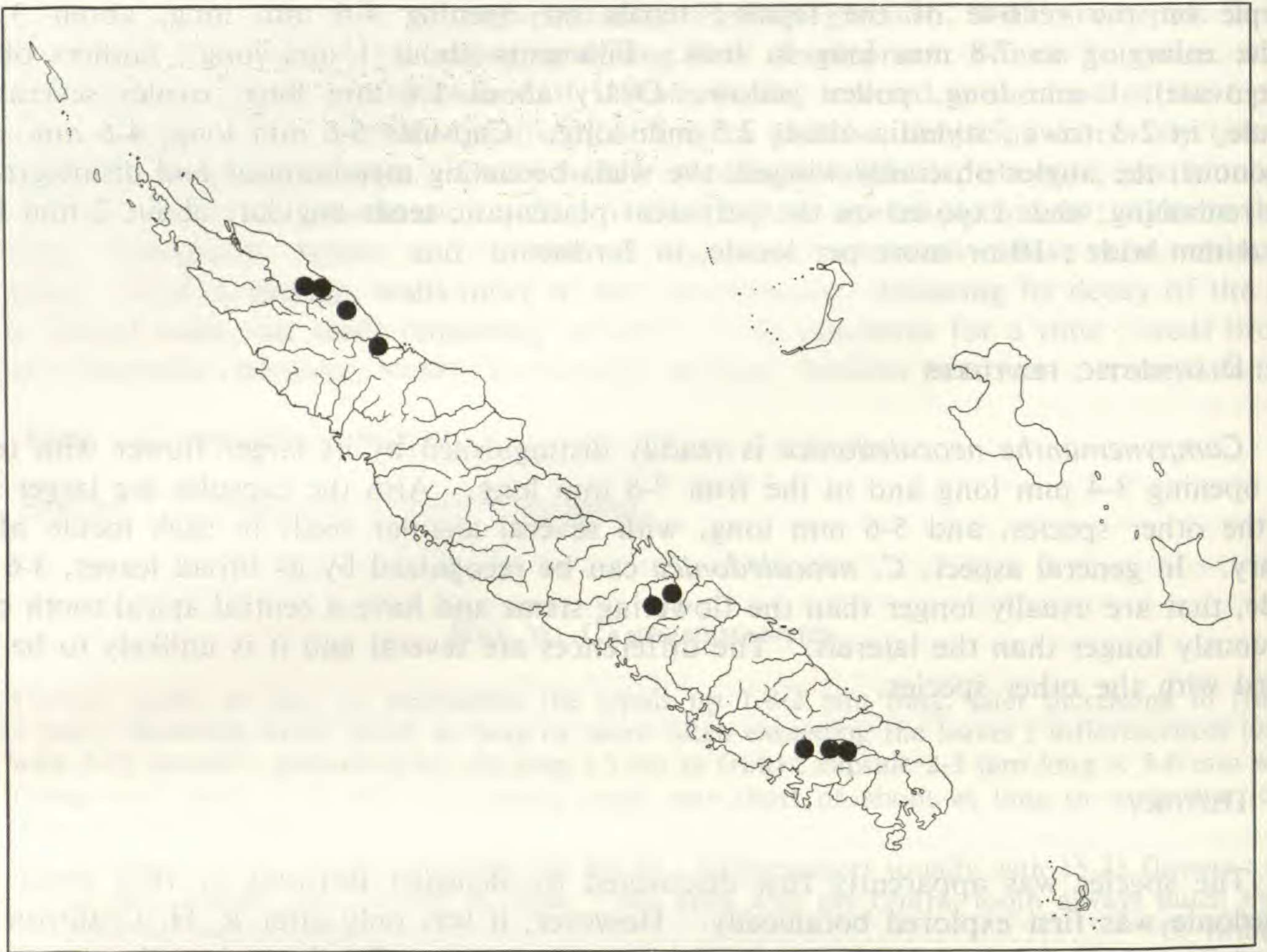


Fig. 1. — Distribution of *Campynemanthe neocaledonica*.

about as long as the laterals. These plants are apparently fertile and the fruits contain 3-5 large irregularly rounded seeds ca. 2 mm in diameter, most like those of *C. viridiflora*. It is possible that it represents a hybrid between *C. neocaledonicum* and *C. viridiflora*. *Campynemanthe neocaledonica* flowers almost throughout the year but there appears to be a peak blooming period from September to December. Fruiting plants have been recorded from April to January.

MATERIAL EXAMINED : NEW CALEDONIA : *Aubréville & Heine 215*, Mgne des Sources, 6.7.1965 (fr.) ; *Balansa 1749*, sud de Canala, vers 1000 m, 11.1869 (fl.) ; *Blanchon 675*, Mgne des Sources, 15.4.1964 (fr.) ; *Compton 1575*, Ignambi, forest at 3500 ft, 1.8.1914 (fl.), syntype ; *1782*, Mt Panié, forest, 1500 ft, 25.8.1914 (fl.), syntype ; *1811*, Mt Panié, forest, 4000 ft, 28.8.1914 (fr.), lectotype ; *Green 1771*, Mt Ignambi, 10 km south of Pouébo, 1000 m, epiphyte on mossy tree trunk, 7.12.1963 (fl., fr.) ; *Lécard s.n.*, Uraï, prairie humide, 500 m, without date (fl.) ; *Lowry 3763*, Mgne des Sources, dense forest, 1000 m, 15.2.1985 (fl.) ; *MacKee 2231*, Mgne des Sources, summit ridge, 1000 m, 10.1955 (fr.) ; *5331*, summit ridge, Mgne des Sources, 23.9.1956 (fl.) ; *8204*, Plateau de Dogny, versant est, 900 m, 18.1.1961 (fr.) ; *13876*, Mt Panié, forest floor, humid forest, 600-800 m, 11.11.1965 (fl.) ; *19156*, Roche Ouaième, Massif de Ton-Ton, 900-980 m, 13.7.1968 (fl.) ; *McPherson 2577*, eastern slope of massif between Diahoué and Yambé, forested slopes, 1000 m, terrestrial, 15.4.1980 (fr.) ; *6584*, Mt Panié, north of Hienghène, forested slopes, 1200 m, terrestrial, 15.5.1984 (fl., fr.) ; *6646*, Plateau de Dogny above Sarraméa, forested slopes, 9.6.1984 (fl., fr.) ; *Raynal & Veillon 16532*,

Mgne des Sources, ca. 1000 m, sous-bois forêt dense de crête, 4.10.1971 (fr. immat.) ; *Schmid 1512*, Mt Panié, vers 950 m, 19.9.1966 (fl., fr.) ; *Veillon 575*, Mt Panié, entre 1000-1500 m, 15.12.1965 (fr.) ; *4273*, crête de l'Ignambi, 15.4.1980 (fl., fr.).

2. *Campynemanthe viridiflora* Baillon

Bull. Mens. Soc. Linn. Paris 2 : 1106 (1893) ; Hist. Pl. 12 : 592 (1894) ; GUILLAUMIN, Fl. anal. et synopt. Nouvelle-Calédonie : 55 (1948).

TYPE : Collector unknown, New Caledonia (holo-, P).

Plants 15-36 cm high. Rhizome relatively slender, to 3 mm in diameter. Leaves 15-25 cm long, 2.5-4 mm wide, apices 3-fid, the central tooth usually much shorter than the laterals (occ. as long or longer than the laterals). Flowering stem longer than the leaves, up to 36 cm long. Inflorescence with about 15-25 flowers ; bracts 6-9 mm long, bracteoles 5-7 mm long ; pedicels about 2(-2.5) cm long, elongating to 3 cm in fruit. Flowers small at anthesis ; tepals pale yellowish-green with darker keels, on opening about 2 mm long, about 0.8 mm wide, enlarging in fruit to 3 mm. Filaments 0.5 mm long ; anthers globose, about 0.5 mm long. Ovary obscure at anthesis, about 1 mm long, ovules few per locule (usually 4), in 2 rows ; stylodia about 1.5 mm long. Capsules broadly obconic, 3-gonous, the angles slightly winged, about 2 mm high, about 6 mm at widest diameter ; locules with 2(-4) seeds, the dorsal walls disintegrating first, exposing the seeds ; seeds \pm rounded and irregularly angled, about 2 mm at the longest, and 1.8 mm in diameter.

DIAGNOSTIC FEATURES

In its general morphology *C. viridiflora* is similar to the other two species of the genus, but it can usually be recognized by its relatively slender flowering stem that is almost always longer than the leaves. In detail it can be distinguished from *C. parva* by its greater height, up to 36 cm, leaf apices with a central tooth much shorter than the laterals, and large fruits, measuring some 6 mm across, containing large globose seeds some 2 mm in diameter. It is less likely to be confused with *C. neocaledonica* which has larger flowers, borne on sturdy flowering stems that are normally somewhat shorter than its comparatively broad leaves. The capsules of *C. neocaledonica* are distinctive being longer than those of *C. viridiflora* and in containing several to many (usually 10 or more per locule) angled, somewhat elongate seeds, up to 2 mm long and 1-1.4 mm wide.

HISTORY

Campynemanthe viridiflora was described in 1893 by BAILLON from rather fragmentary material that constitutes the supposed type of the species in the Paris Herbarium. The original collector and the date and precise origin of the specimen is not recorded. It is likely that BAILLON detached the parts in the type collection from one or more of the several specimens in the Paris Herbarium that had been collected by BALANSA, VIEILLARD, RAOUL and

others. *Campynemanthe viridiflora* has been collected repeatedly this century but at a limited number of localities in the southern third of the island. It is the type species of *Campynemanthe* and until now was regarded as the only member of the genus.

DISTRIBUTION AND HABITAT

The species is restricted to the southern third of New Caledonia where it occurs in moist shady forested sites above 850 m (Fig. 2). As mentioned under *Campynemanthe neocaledonica*, putative hybrids with the latter have been recorded at Mt Mou and Mgne des Sources. *Campynemanthe viridiflora* also grows in the same areas as *C. parva* but it is not known whether the two species occupy the same or different habitat niches. *Campynemanthe viridiflora* has been collected in flower and fruit at all times of the year but the peak blooming period seems to be December to April.

MATERIAL EXAMINED : NEW CALEDONIA : *d'Alleizette* 491, Yahoué, 11.1910 (fl., fr.) ; *Balansa* 1750, Mt Humboldt, vers 1000 m. 12.10.1869 (fr.) ; 2931 Mt Mou, vers 1100 m, 4.1870 (fl.) ; *Bernier* 1316, sommet du Mt Mou (Païta), 1200 m, 12.1902 (fl.) ; *Blanchon* 349, Pic des Mousse, forêt

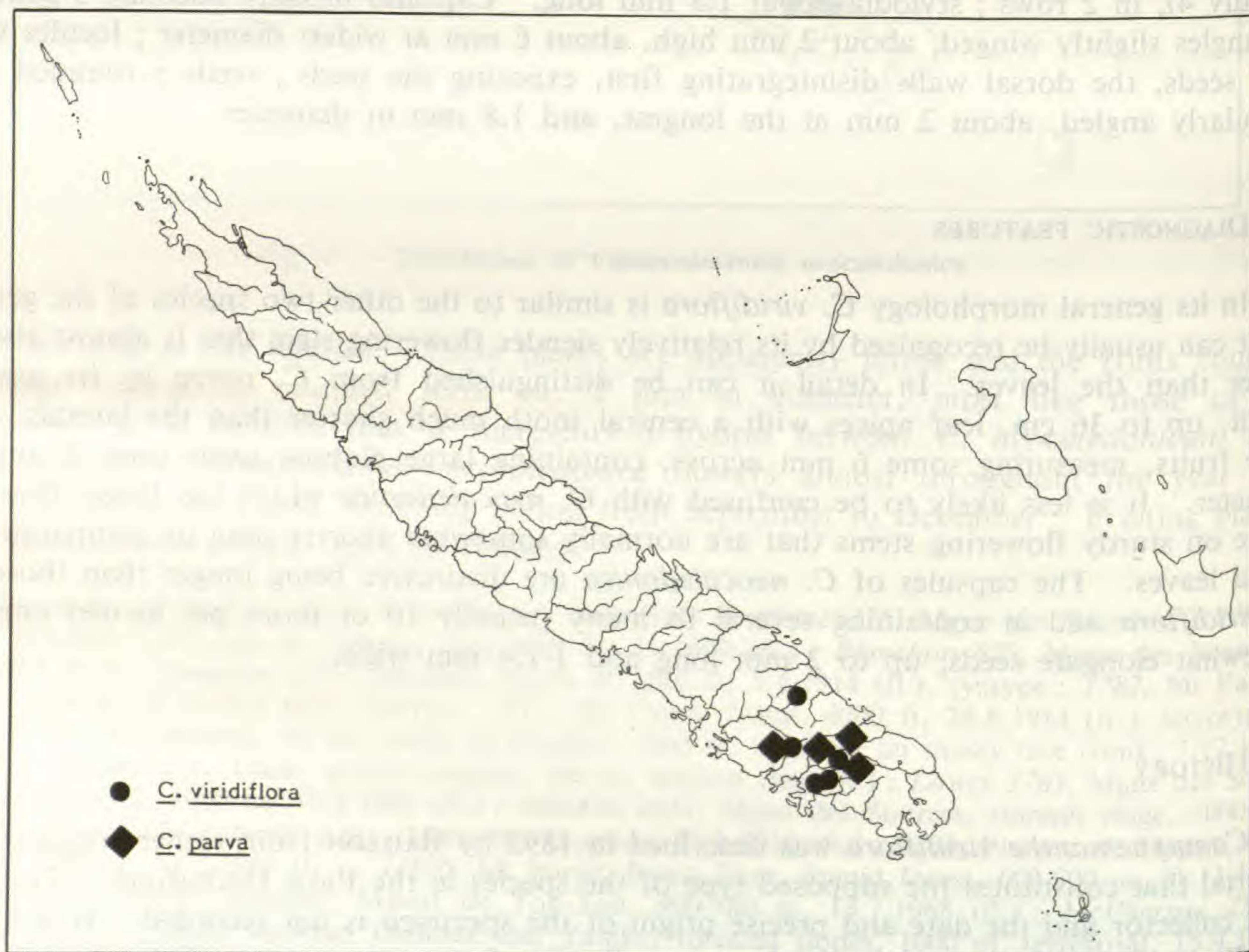


Fig. 2. — Distribution of *Campynemanthe viridiflora* and *C. parva*.

hygrophyle, 27.8.1963 (late fl., fr.); *Brinan 1056*, Humboldt Massif, 1200 m, moss forest, 19.12.1980 (fl.); *1098*, Mt Humboldt, 1300 m, 21.12.1980 (late fl., fr.); *Brousmiche 488*, marais à la Concepcion (possibly incorrect locality), 27.3.1881 (fl., fr.); *Compton 573*, Mt Mou, serpentine forest, 2500 ft, 15.3.1914 (fl.); *729*, Mt Koghi, scrub forest, 3000 ft, serpentine, 10.4.1914 (fl.); *Deplanche 127*, Mgne de Mou, 1200 m, 23.7.1863 (fr.); *Green 1270*, summit of Mt Mou, rocky montane mist forest, 7.10.1963 (fl.?, fr.); *Hoff 2638*, Mt Humboldt, 1350 m, 19.9.1980 (fr.); *Jaffré 1995*, Mt Humboldt, 1450 m, 13.10.1977 (fr.); *Le Rat 39*, Mt Mou, 1219 m, 7.1909 (fl., fr.); *Lowry 3762*, Mgne des Sources, 1000 m, dense forest, 15.2.1985 (fl.); *Lowry & Suprin 3812*, Mt Humboldt, low forest along trail from Tontouta R. valley, 1350 m, 22.2.1985 (fl.); *MacKee 3803*, Mt Mou, summit ridge, 21.1.1956 (fl.); *McPherson 1715*, Mgne des Sources, low forest on plateau, ca. 850 m, 28.6.1979 (fr.); *4707*, Mt Mou, forested slopes north of Païta, ca. 1150 m, 21.7.1982 (fr.); *5106*, Mt Humboldt, low forest near summit, 12.11.1982 (fl., fr.); *6608*, Mt Mou, near Païta, 24.5.1984 (fr. immat.); *6609*, *ibid.*, 1100 m, 24.5.1984 (fl.); *Morat 5168*, Mt Humboldt, 1300 m, épiphyte-terrestre près de la mare en forêt, 4.11.1976 (fr.); *Raoul s.n.*, sud de N. Calédonie, 19.12.1889 (fl.); *Schlechter 14917*, Bergen bei Païta, 1250 m, 5.10.1902 (fl., fr.); *Schmid 4942*, Mgne des Sources, vers 1100 m (fl.); *Vieillard 3322*, Mt Mou, summit, 1866 (fl.); *Veillon 299*, Mt Mou, petite forêt vers 1100 m, 30.7.1965 (fr.); *Viot 289*, Mt Mou, ± 1100 m, 21.8.1940 (fr.).

3. *Campynemanthe parva* Goldblatt, *sp. nov.*

Planta 6-15 cm alta, foliis 5-15 cm longis, 2-2.5 mm latis, dentibus apicalibus ± aequalibus vel interiore longiore; inflorescentia 7-15 florum, tepalis 1.8-2 mm longis, increscentibus in fructo ad 2.5 mm, capsulis ca. 2 mm longis, 3 mm latis, seminibus usitate 4 in loculo quoque, ca. 1 mm × 0.5 mm.

TYPE : *MacKee 9751*, New Caledonia, vallée de la Ouinné, on rocks in shade, 300 m (holo-, P; iso-, NSW). — Fig. 3.

Plants 6-15 cm high. Rhizome 2-3 mm in diameter. Leaves 5-15 cm long, 2-2.5 mm wide, apices 3-fid, the teeth ± equal or the inner somewhat longer. Flowering stem about as long as the leaves, 6-15 cm long. Inflorescence with 7-15 flowers; bracts 5-7 mm long, bracteoles 4-5 mm long; pedicels 0.8-1.2 cm long, elongating to 1.8 mm in fruit. Flowers small to medium in size; tepals on opening 1.8-2 mm long, about 1 mm wide, enlarging to 2.5 mm long in fruit. Filaments nearly 1 mm long; anthers globose, almost 0.5 mm long. Ovary about 0.5 mm long, ovules several per locule; stylodia ca. 1 mm long. Capsules obconic, about 2 mm long, 3 mm at the widest, eventually dehiscent loculicidally, the walls becoming membranous and decaying but the seeds remaining attached to the placentas; seeds small, angular, usually 4 per locule, about 1 mm long, 0.5 mm wide.

DIAGNOSTIC FEATURES

The distinguishing features of *Campynemanthe parva* are its small size, rarely over 12 cm high, small flowers with the tepals about 2 mm long on opening and enlarging to 2.5 mm in fruit. The short obconic capsules are ca. 2 mm long and contain small, strongly angular seeds about 1 mm long. The flowering stem is typically about as long as the leaves and the leaf apices have more or less equal teeth or the inner tooth is somewhat longer than the laterals.

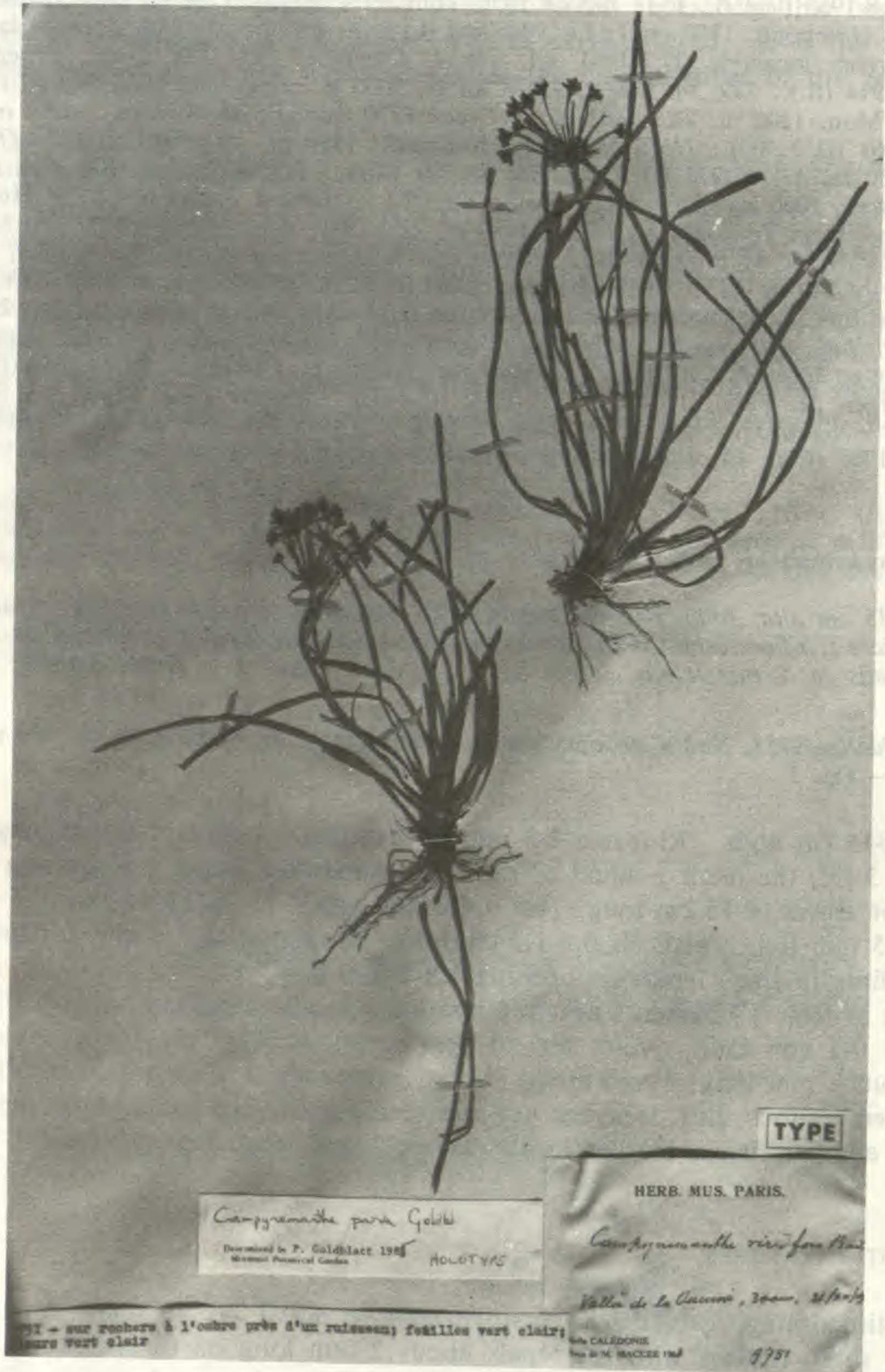


Fig. 3. — The type specimen of **Campynemanthe parva** in the Paris Herbarium. (MacKee 9751, New Caledonia, Vallée de la Ouinné).

DISTRIBUTION AND HABITAT

Campynemanthe parva is recorded from mid to upper elevations in the southern third of New Caledonia (Fig. 2) and like the other species of the genus it is found in mesic forested habitats. It is the most geographically restricted of the three species of *Campynemanthe* and it was the last to be discovered, the first collections that I have seen being made by Robert VIROT in 1938. *Campynemanthe parva* is very localized, occurring only in the Mt Mou — Rivière Bleue — Mt Dzumac area. It occurs in the same localities as *C. diflora* at Mt Mou and Mgne des Sources. There is no information as to whether they grow together or in different habitats. Flowering appears to be limited to November to April but this may be an artifact due to incomplete collecting of the species. Fruiting plants have been collected from November to August.

MATERIAL EXAMINED : NEW CALEDONIA : *Aubréville & Heine 158*, Rivière Bleue, 1.7.1965 (fr.) ; *Blanchon 669*, Vallée Ouinné, serpentine among boulders, 3.3.1964 (fl., fr. immat.) ; *1254*, Mt Dzumac, vers 1000 m, 6.12.1964 (fl.) ; *MacKee 9751*, Vallée de la Ouinné, 300 m, on rocks in shade next to stream, 28.12.1962 (fl.) ; *32270*, Haute Ouinné, 600 m, 18.11.1976 (fr.) ; *McPherson s.n.*, Mt Mou, 10.1983 (fr.) ; *Stauffer & Blanchon 5748*, Mt Dzumac, Ouinné-Tal, *Agathis lanceolata* forest, ca. 620 m, 3.3.1964 (fr. immat.) ; *Veillon 3042*, Haute Ouinné, vers 700 m, 28.4.1974 (fl., fr.) ; *3346*, Rivière Bleue, 300 m, 21.11.1977 (fl.) ; *Virot s.n.*, sud du Pic du Roches, 800 m, 5.1938 (fr.) ; *Webster & Hildreth s.n.*, Mgne des Sources, ca. Dumbéa, ravine in montane rain forest, 800 m, 22.8.1968 (fr.).

2. **CAMPYNEMA** Labill.

Novae Holland. Pl. Specimen 1 : 93-94 (1805) ; R. BR., Prod. Fl. Novae Hollandiae 1 : 146 (1827) ; HOOKER, Fl. Tasmaniae 2 : 48 (1858), in Antarctic Voyage of Erebus and Terror 3 ; BENTHAM, Fl. Australiensis 6 : 415 (1873) ; BENTHAM & HOOKER, Gen. Pl. 3 (2) : 760 (1883) ; RODWAY, Tasmanian Flora : 210 (1903).

— *Campylonema* SCHULTES F., Syst. Veg. 7 : 1507 (1830), orth. var.

Plants herbaceous perennials with the rootstock a tufted crown, the roots somewhat fleshy. Cataphylls few, membranous, basal, reaching to ground level. Leaves few, the lowermost inserted on the stem above the base, near ground level, and largest, lanceolate, with an open sheath below, other leaves smaller, decreasing in size upwards. Flowering stem erect, unbranched. Inflorescence 1-3(-4)-flowered, subtended by a basal bract and the lateral flowers if present each bearing a smaller bract shortly below the flower. Flowers actinomorphic, green ; tepals lanceolate, subequal, persistent and enlarging in fruit, lacking apparent nectaries. Stamens 6, in two distinct whorls, the outer 3 somewhat longer than the inner, inserted at the base of the tepals, filaments slender, initially erect but becoming recurved after dehiscence ; anthers nearly versatile, the filaments inserted just below the midline, dehiscing latero-extrorsely. Ovary barely swollen at anthesis, rapidly elongating after fertilization, trilocular, placentation axile ; stylodia free but thickened and contiguous below. Fruit dry, often referred to as a capsule but probably indehiscent ; seeds numerous, pale straw colored, the outer coat spongy, flattened and crescentic to discoid.

TYPE : *C. lineare* Labill.

SPECIES : 1 only, restricted to Tasmania.

The outstanding features that separate *Campynema* from *Campynemanthe* are its large single sub-basal leaf and simple few-flowered inflorescence in stark contrast to the many basal leaves and compound umbel-like inflorescence of *Campynemanthe*. To these obvious differences can be added several more including an entire acute leaf apex, lack of a rhizome, multi-ovulate ovary, and seeds with a spongy outer coat. The primary embryological features of the two genera correspond well but differences such as a multinucleate tapetum versus 2-nucleate in *Campynemanthe* and sulcate pollen grains (inaperturate in *Campynemanthe*) reinforce the morphological differences. There can be no doubt that *Campynemanthe neocaledonica*, initially referred to *Campynema*, does not belong here. It is consistent in every significant character with *Campynemanthe*, including all those listed here. *Campynema* is thus monotypic and restricted to Tasmania.

Campynema and *Campynemanthe* probably share sufficient similarities that they should be considered related genera. Their affinities are uncertain and treatment in a separate *Campynemataceae* seems most appropriate given the incomplete state of our knowledge about them.

1. *Campynema lineare* Labill.

Novae Holland. Pl. Specimen 1 : 94 (1805) ; BENTHAM, Fl. Australiensis 6 : 415 (1873) ; RODWAY, Tasmanian Flora 210 (1903).

— *Campynema pygmaeum* F. MUELL. ex BENTH., Fl. Austral. 6 : 415 (1873) ; type : *Oldfield s.n.*, Tasmania, summit of Mt Lapeyrouse (MEL, possible isotype).

LECTOTYPE : *Labillardière s.n.*, Tasmania (G).

Plants (3-)6-20 cm high. Leaves about as long as the stem (esp. small plants) to half as long, 2-12 cm long, 3-9 mm wide. Flowers green ; tepals at anthesis about 5-7 mm long, increasing to 8-10 mm in fruit. Filaments slender, 1-2 mm long, strongly recurved after dehiscence ; anthers oblong, 0.8-1.4 mm long. Ovary barely swollen at anthesis, ca. 2 mm long, rapidly elongating after fertilization, stylodia initially ca. 1 mm long, about 2 mm immediately after fertilization, contiguous below. Capsule (8-)12-18 mm long, turbinate to linear-oblong, tapering towards the base ; seeds more or less oval, to 2 mm at the longest axis.

VARIATION

Plants vary considerably in size, and even single collections may comprise a range of specimens from 5-15 cm high. The smaller individuals are apparently from exposed and often alpine sites. The species *C. pygmaeum* ascribed to F. MUELLER by BENTHAM (1873), is currently regarded as a reduced alpine form (RODWAY, 1903), a treatment consistent with the overall pattern of variation evident in the available collections of *Campynema*.

HISTORY

Campynema lineare was first collected by the naturalist, Jacques Julien LABILLARDIÈRE in the early 1790s. LABILLARDIÈRE was one of the scientists that accompanied the French expedition sent to the Pacific in search of the ill-fated La Peyrouse Expedition that had gone to Australia in 1785 and was lost sometime in 1788. Although Labillardière's expedition found no trace of LA PEYROUSE, he and his colleagues made numerous collections and their discoveries in Tasmania and Western Australia rank high in the history of botanical exploration in Australia. *Campynema lineare* has been recollected relatively frequently and it is apparently not uncommon in the parts of Tasmania where it occurs.

DISTRIBUTION AND HABITAT

Campynema lineare is largely confined to the western half of Tasmania where it occurs from near sea level to altitudes of up to 900 m. It is apparently most common in the southwest from Strahan to Port Davey and inland to Mt Field. Habitats range from grassy meadows at lower elevations to wet rocky cliffs and alpine sites where *C. lineare* grows among heath and cushion plants. The dwarf form is restricted to the most exposed and highest sites recorded for the species. *Campynema lineare* blooms from December to March.

MATERIAL EXAMINED : TASMANIA : Adams 40, Moores Garden, 880 m, among cushion plants, no date (fl.) ; Ashton s.n., Cradle Valley, 3.1960 (fl.) ; Barber s.n., National Park, 42°41' × 146°43', March (fl.) ; Buchanan 443, Sharlands Peak, western slopes, Frenchmans Cap Track, January (fl.) ; 3044, SW end of Moonlight Ridge above 870 m, reservoir lakes, alpine cushion herb field, no date (fl.) ; 3404, S. coast track, W. slope Ironbound Range, crack in cliff, 400 m, April (fl.) ; Davis 1174, Melaleuca Settlement, no date (fl.) ; 1417, Bathurst Harbour, Port Davy, sea level, wet plains, 11.3. 1954 (fl.) ; Giblin s.n., Lake Fenton, National Park, 3.1928 (fl.) ; Gulliver s.n., Petrarch, 3.1873 (fl.) ; Harwood s.n., Denison Range, Reeds Park area, 12.1978 (fl.) ; Milligan 1004, Turnbull's and Middle-sen Plains, 25 mi. S. Ulverstone Farm, no date (fl.) ; Moscal 144, Mt Counsel, open alpine heath, 600-800 m, March (fl.) ; 968, cliff near waterfall, seepage area in shade E. of Lake Picone, March (fl.) ; Mulligan 762, Mt Sorell, Macquarie Harbour, 15.1.1847 (fl.) ; Perrin s.n., Pelion Plateau, 1.1922 (fl.) ; Rodway s.n., Mt Field. 3.1982 (fr.) ; Mt Roland 2.1906 (fl.) ; 198, Southport, 4.1985 (fr.) ; Scott s.n., W. Tasmania, 1890 (fl.) ; Stones s.n., Mt Field National Park, January (fl.) ; Stuart 1832, South Port, 2.1856 (fl.) ; Sutton s.n., Dove River, January (fl.).

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LITERATURE CITED

- AMBROSE, J. D., 1980. — *A re-evaluation of the Melanthioideae (Liliaceae) using numerical analyses.* In BRICKELL, C. D. et al. (editors), *Petaloid Monocotyledons* 65-81. Academic Press, London.
- BAILLON, H., 1893. — L'organisation et les affinités des Campynemées. *Bull. Mens. Soc. Linn. Paris* 2 : 1105-1109.

- BAILLON, H., 1894. — *Histoire des Plantes* 12. Hachette, Paris.
- BENTHAM, G., 1873. — *Flora Australiensis* 6. Reeve & Co., London.
- BENTHAM, G. & HOOKER, J. D., 1883. — *Genera Plantarum* 3 (2). Reeve & Co., London.
- CHEADLE, V. I., 1968. — Vessels in Haemodorales. *Phytomorphology*. 18 : 412-420.
- DAHLGREN, R. & CLIFFORD, H. T., 1982. — *The Monocotyledons : A Comparative Study*. Academic Press, London.
- DAHLGREN, R. & RASMUSSEN, F., 1983. — Monocotyledon evolution : characters and phylogenetic states. *Evol. Biol.* 16 : 255-388.
- DAHLGREN, R., CLIFFORD, H. T. & YEO, P., 1985. — *The Families of the Monocotyledons : Structure, Evolution and Taxonomy*. Springer-Verlag, Heidelberg.
- DAHLGREN, R. & AN-MING, LU, 1985. — The genus *Campynemanthe* (Campynemaceae) : morphology, microsporogenesis, early ontogeny and relationships. *Nordic J. Bot.* 5 : 321-330.
- DE VOS, M. P., 1961. — On the embryology and relationships of the South African genera of the Haemodoraceae. *Recent Advances in Biology. IX International Botanical Congress, Montreal, 1959*. University of Toronto Press, Toronto.
- DUMORTIER, B.-C., 1829. — *Analyse des Familles des Plantes*. Casterman, Tournay.
- DUTT, B. S. M., 1970. — Hypoxidaceae. *Bull. Indian Nat. Acad. Sci. Acad.* 41 : 368-372.
- ERDTMAN, G., 1952. — *Pollen Morphology and Plant Taxonomy*. Almqvist & Wiksell, Stockholm.
- GOLDBLATT, P., HENRICH, J. E. & RUDALL, P., 1984. — Occurrence of crystals in Iridaceae and allied families and their phylogenetic significance. *Ann. Missouri Bot. Gard.* 71 : 1013-1020.
- GUILLAUMIN, A., 1948. — *Flore Analytique et Synoptique de la Nouvelle-Calédonie : Phanérogames*. Office de la Recherche Scientifique Coloniale, Paris.
- HOOKE, J. D., 1860. — *Florae Tasmaniae* 2. Lovell Reeve, London.
- HUBER, H., 1969. — Die Samenmerkmale und Verwandtschaftsverhältnisse der Liliiflorae. *Mitt. Bot. Staatssamml. München* 8 : 219-538.
- HUTCHINSON, J., 1959. — *The Families of Flowering Plants*, Ed. 3. Clarendon Press, Oxford.
- LABILLARDIÈRE, J.-J., 1805. — *Novae Hollandiae Plantarum Specimen*. 1. Huzard, Paris.
- MELCHIOR, H., 1964. — In ENGLER, A. & PRANTL, K., *Syllabus der Pflanzenfamilien* 2. Borntraeger, Berlin.
- PAX, F., 1888. — Amaryllidaceae. In ENGLER, A. & PRANTL, K., *Die Natürliche Pflanzenfamilien*, ed. 1, 2 (4) : 97-124. Engelmann, Leipzig.
- PAX, F. & HOFFMANN, K., 1930. — Amaryllidaceae. In ENGLER, A. & PRANTL, K., *Die Natürliche Pflanzenfamilien*, ed. 2, 15A : 391-430. Engelmann, Leipzig.
- RENDLE, A. B., BAKER, E. G. & MOORE, S. L., 1921. — A systematic account of the plants collected in New Caledonia and the Isle of Pines by Prof. R. H. Compton, M. A., in 1914. Part 1. Flowering plants (Angiosperms). *J. Linn. Soc., Bot.* 45 : 245-263.
- RODWAY, L., 1903. — *The Tasmanian Flora*. Government Printer, Hobart.
- TAKHTAJAN, A. L., 1980. — Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.* 46 : 225-359.